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THE VERTICAL DISTRIBUTION AND REPRODUCTIVE BIOLOGY OF *PELOGOBIA LONGICIRRATA* (ANNELIDA) IN THE CENTRAL ARCTIC OCEAN

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Although holopelagic polychaetes are widely distributed throughout the oceans, very little quantitative information exists on their vertical distribution and even less is known of their reproductive biology and life histories. Most of our knowledge on these subjects comes from the many expeditions and surveys of the last one hundred years which, although of great importance in many respects, are of limited value for analytical evaluations and comparisons. This is due to differences in the type of collecting gear and sampling methods employed and in the depths sampled, and the fact that most cruises covered too wide a geographic range to intensively study any one area over an extended period of time. As a result the information which can be obtained on any particular species from a review of such data is necessarily incomplete and sometimes even contradictory. More recent quantitative approaches to plankton analysis have not increased our knowledge either, since they have generally not included pelagic polychaetes. Of the few studies on holopelagic polychaetes in which closing nets have extensively been used, Mileikovsky (1969 and 1962), Tebble (1960), Friedrich (1950), and Hardy and Gunther (1935) deserve special mention. Of the polychaetes studied by them, one of the most abundant was *Pelogobia longicirrata* Greeff 1879, a cosmopolitan species which reaches a maximum length of approximately 12mm in 26 to 30 segments and has been collected from below 4000m to the surface and throughout the world: Støp-Bowitz, 1948 (north Atlantic); Friedrich, 1950 (Atlantic); Tebble, 1960 (south Atlantic); Hardy and Gunther, 1935 (South Georgia); Augener, 1929 (Weddell sea); Berkeley and Berkeley, 1964 (Peru); Dales, 1957 (central Pacific); Tebble, 1962 (north Pacific); Mileikovsky, 1969 (northwest Pacific); and Okuda, 1937 (Japan). For a more complete listing of the literature concerning this species the reader should see Dales (1972).

P. longicirrata is also present in the central Arctic ocean (Uschakov, 1957; Knox, 1959; and Yingst, 1972) and was the most abundant holopelagic polychaete collected in a two year program of systematic plankton sampling conducted from Fletcher's Ice Island T-3. This paper presents data from that two year study on the reproductive biology and vertical distribution of the larvae, juveniles, and adults of *P. longicirrata* and proposes a life history for this species. Fletcher's Ice Island T-3 served as a stable working platform which permitted long term quantitative sampling with closing nets in a restricted oceanic region and thereby allowed researchers to amass the type of data so difficult to obtain by more conventional means in the open sea. Likewise, the direct development of the larvae of *P. longicirrata* into a form clearly recognizable and comparable with the adults (Nolte, 1938) has facilitated this study. Since *P. longicirrata* is an abundant cosmopolitan species, it is hoped that this Arctic study will also be of general interest to those concerned with the distribution and natural history of holopelagic polychaetes in other seas.

Materials and Methods

A one meter closing net with a number 6 mesh (215 μ opening) was used to sample discrete vertical intervals from 0 to 1500 m in the central Arctic basin. All sampling was done by oceanographic teams from the University of Southern California and the University of Washington from Fletcher's Ice Island T-3, while the island drifted from 84° 24′N, 112° 30′W (March, 1970) to 84° 20′N, 86° 17′W (December, 1971). Complete series of tows from 0 to 1500 m were taken an average of 2 or 3 times a month from March, 1970 to November, 1971 with the exception of September, October and November, 1970. During 1970 the upper 300 m (0–300 m) was sampled in 50 m increments; successive tows of 200 m were taken from 300 m to 900 m followed by 300 m tows from 900 m to 1500 m. In 1971 the sampling program from 0 to 500 m was modified, such that 25 m tows were taken from 0 to 400 m, and 100 m tows from 400 m to 500 m. For purposes of this report, data in the upper 500 m from both years was pooled to give three intervals: 0–100 m, 100–300 m, 300–500 m. Thus, a complete series of tows from 0 to 1500 m includes the following: 0–100 m, 100–300 m, 300–500 m, 500–700 m, 700–900 m, 900–1200 m, 1200–1500 m. All data presented here are from complete series of tows with the exception of July/August, 1970 when there were no tows from 1200–1500 m and December, 1970 when the results from one complete series from 0–1500 m were extrapolated to a partial second series extending from 0 to 700 m. In this case, the same number of specimens found in each size class and in each depth interval from 700 m to 1500 m in the complete series was added to the data from the partial series from 0 to 700 m. The net result is the adjusted equivalent of two complete series for December, 1970.

Each tow was fixed and preserved in 10% formalin in seawater. Later, the USC Arctic project personnel sorted the animals to phylum and gave the annelids to the author who identified them to species. The total number of complete specimens and fragments bearing a prostomium of *P. longicirrata* were then counted and separately recorded for each tow. Likewise, the number of true segments (the entire worm excluding the prostomium and the pygidium) was determined for each complete specimen in a given tow. On the basis of its number of true segments, each animal was placed in one of 8 size classes. Each class contained specimens in a three segment range, so that the first group included specimens with 1 to 3 segments, the second those with 4 to 6 segments, and the eighth those with 22 to 24 segments.

In order to compare the vertical distribution of the size classes throughout the year, the above data for each vertical tow were grouped into the depth intervals previously noted and pooled for a two month period. Due to the differences in the lengths of the depth intervals comprising the series of tows from 0–1500 m, the volume of water filtered by the net varied considerably from interval to interval. To remove this volume bias in comparing the data in the different intervals, the number of animals in each size class in the 100 m intervals was multiplied by 3 and those in the 200 m intervals by 1.5, so that the volume of water equalled the amount filtered in the largest intervals of 300 m. After this correction, the number of animals in each size class at each depth was determined as a percentage of the total number of complete specimens in a given two month period.

The above manipulation of the volume filtered was possible because the filtering efficiency of the net was not found to vary considerably between tows. The filtering efficiency was calculated by dividing the amount of water actually filtered by the net (as measured by a flow meter) by the maximum theoretical filtering capacity of the net. The ratio averaged approximately 0.5.

The average density of animals from 0–1500 m was calculated by dividing the total number of complete and incomplete specimens in a two month period by the total volume of water filtered by the net, as calculated from the filtering efficiency and the length of the tow.

Oocytes were counted through the body wall under a compound microscope and measured with an ocular micrometer. If an animal had a minimum of 4 oocytes in each of at least 3 segments, it was recorded as being ovigerous. The total number of ovigerous animals taken in a given two month period was then figured as a percentage of all the specimens with more than 12 segments in that time period. Larvae are defined here for convenience as specimens with 6 or less segments, juveniles those with 7 to 12 segments, and adults those with 13 or more segments.

Results

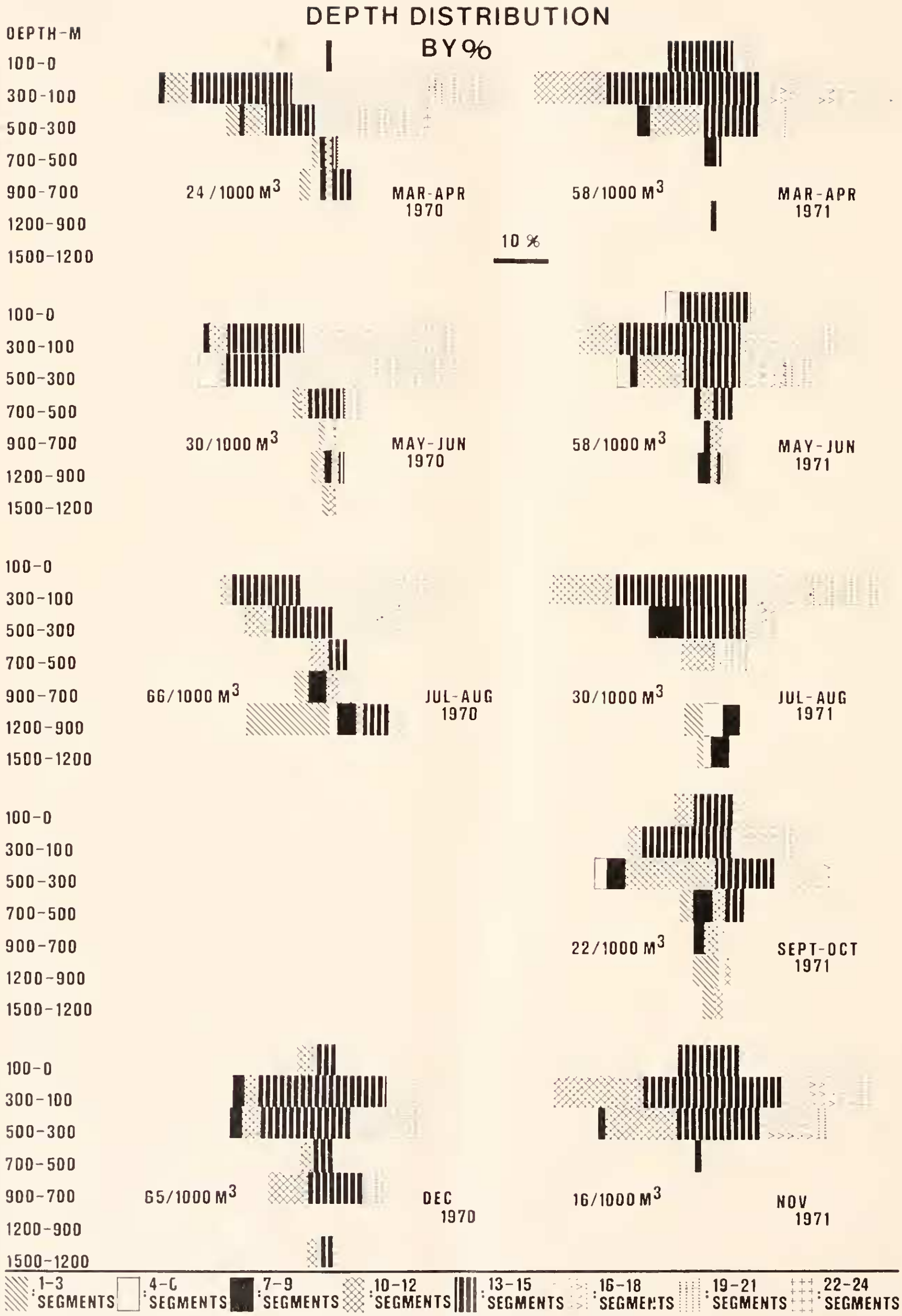
Vertical distribution and relative age

The vertical distribution of *P. longicirrata* changed seasonally as a function of the relative age of the specimens (Fig. 1). Animals with 13 or more segments were primarily found above 500 m where at least 60% of the total population was collected throughout the year in any given two month period. During the summer (and early fall) the percentage of animals under 500 m increased, reaching a maximum between July and October (Fig. 1). In contrast to those above, most of the individuals below 500 m had less than 13 segments. In fact, those with the fewest number of segments were found the deepest. For example, specimens with 1 to 3 segments were primarily found below 900 m and made up most of the population from 900 m to 1200 m (Fig. 1).

Density

The average density of animals from 0–1500 m fluctuated somewhat during the two year sampling period, but did so without demonstrating any apparent seasonal trends (Fig. 1). The mean density for 1970 and 1971 was 46/1000 m^3 and 37/1000 m^3, respectively.

The following is a list of the number of complete series of tows from 0–1500 m, the numbers of whole specimens (ws), and fragments bearing a prostomium (f) collected in a given two month period: March/April, 1970 (ws = 158, f = 30, 13 series from 0–1500 m); May/June, 1970 (ws = 71, f = 21, 5 series from 0–1500m); July/August, 1970 (ws = 73, f = 53, 4 series from 0–1200 m); December, 1970, (ws = 54, f = 8, 1 series from 0–1500 m, and 1 series from 0–700 m); March/April, 1971 (ws = 90, f = 14, 3 series from 0–1500 m); May/June, 1971 (ws = 106, f = 28, 4 series from 0–1500 m); July/August, 1971 (ws = 38, f = 52,


DEPTH DISTRIBUTION
BY %
DEPTH-M
100-0
300-100
500-300
700-500
900-700
1200-900
1500-1200
24/1000 M3
MAR-APR 1970
58/1000 M3
MAR-APR 1971
10 %
30/1000 M3
MAY-JUN 1970
58/1000 M3
MAY-JUN 1971
66/1000 M3
JUL-AUG 1970
30/1000 M3
JUL-AUG 1971
22/1000 M3
SEPT-OCT 1971
65/1000 M3
DEC 1970
16/1000 M3
NOV 1971
1-3 SEGMENTS
4-6 SEGMENTS
7-9 SEGMENTS
10-12 SEGMENTS
13-15 SEGMENTS
16-18 SEGMENTS
19-21 SEGMENTS
22-24 SEGMENTS

5 series from 0–1500 m); September/October, 1971 (ws = 47, f = 6, 4 series from 0–1500 m); and November, 1971 (ws = 17, f = 3, 2 series from 0–1500 m).

Occurrence of oocytes

With the hope of defining the breeding season and the development of sexual maturity in *P. longicirrata*, the occurrence of oocytes throughout the sample population was investigated. Oocytes as viewed through the body wall with a compound microscope were opaque, either spherical or ovoid, and contained a large amount of yolk. In general they were similar to the oocytes of this species shown by Reibisch (1895).

Oocyte diameters ranged from 8 μ to 120 μ, but most were between 20 μ and 40 μ. The ratio of the yolk diameter to the total oocyte diameter decreased from 0.7 in oocytes with a diameter of 20 μ to 40 μ to about 0.4 in the 60 μ to 120 μ range. These data, however, do not suggest at what size the oocytes are sexually mature or even what diameter constitutes a maximum size for this species. Occasionally, the coeloms of the middle segments of specimens were densely packed with 30 to 40 oocytes per segment. In most specimens, however, the oocyte density was 6 to 10 per segment in each of 5 to 10 of the middle segments. Of the 104 specimens which contain a minimum of 4 oocytes in each of at least 3 segments, 82% had 15 to 20 segments. No oocytes were visible in specimens with less than 13 segments. Thus, on this basis, the breeding population is probably comprised of animals wth 15 or more segments.

As to seasonal variations in numbers, the peak occurrence of oocytes in both years was in the two month period of May/June when 30% of those with more than 12 segments bore oocytes (Fig. 2). The rapid decline in percentages from May/June to July/August suggests that spawning took place in early summer.

Developmental features concerned with food procurement

Specimens with more than 5 segments were found to have a mouth, anus, a continuous digestive tract, and a muscled pharynx which was often everted. Although these eversions were probably evoked during fixation of the specimens, they do indicate a capacity for eversion, a necessary prerequisite for feeding. On the other hand, the digestive tracts of animals with two or three segments were incomplete and appeared to be restricted to the anterior half of the body. Well preserved specimens of this size, very similar to the figure shown by Mileikovsky (1970), had a dense opaque area in the anterior half. Such an area could indicate the presence of yolk, which may play an important role in the survival of the larvae below 900 m. As an adult, *P. longicirrata* does not develop jaws on its proboscis which implies that it is not carnivorous.

FIGURE 1. The corrected annual vertical distribution of *P. longicirrata*. The specimens were placed into 8 size classes based on the number of segments. Each size class is coded by a different type of shading. The horizontal length of the bars is proportional to the relative number of specimens from each depth interval and in each size class in a two month period. The solid black line near the top of the figure is equivalent to a 10% contribution. The numbers on the lower left side of each two month distribution represent the average density from 0 to 1500 m for the two month period.

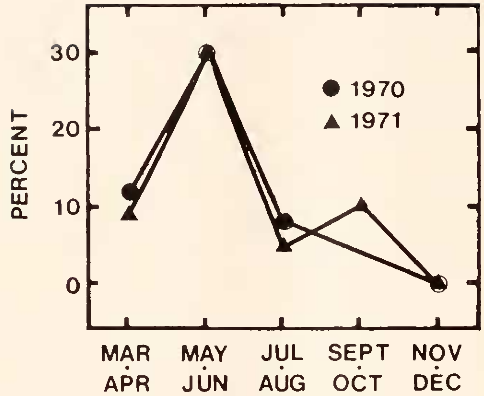


FIGURE 2. The percentage of specimens with 13 or more segments in a given two month period possessing a minimum of 4 oocytes in each of at least 3 segments. There are no data for the period of September–October, 1970.

Discussion

Although it appears that *P. longicirrata* spawns during the late spring and early summer, it is doubtful that spawning is restricted to this period, as evidenced by the presence of some specimens with oocytes as early as March/April and as late as October (Fig. 2) and the occurrence of at least a few larvae for as much as 6 months of the year (Fig. 1). Since the breeding population is chiefly composed of animals living from 100 m to 500 m and very few ovigerous specimens were found below 500 m, spawning probably occurs above 500 m. At present nothing is known about fertilization or the subsequent fate of the spawners. It is possible, however, that females could either spawn more than once or shed the eggs or embryos over an extended period of time. According to Goodrich (1945) the Phyllodocidae, which at that time included the genus *Pelogobia*, possess a protonephromixium which generally provides a duct through which genital products can be shed. If *P. longicirrata* has such nephromixia, it is unlikely that the body wall would have to be ruptured and the female sacrificed to release the ova or embryos. However they are released, these ova or embryos evidently descend from the surface because most larvae are first found between 900 m and 1200 m. It is doubtful that the larvae feed at these depths; instead, they probably live on stored yolk retained from the egg. As they mature and slowly develop the morphology necessary for feeding, the juveniles move up in the water column. This upward movement occurs during and just after the yearly phytoplankton bloom in July and early August (English, 1961).

Although it was not appreciated at the time, the occurrence of the larvae below the adults may have been indirectly confirmed for *P. longicirrata* by two former studies. In the first, no larvae or juveniles were found during the summer in the upper 500 m of the Norwegian and Barents sea, although adults were numerous in this range (Mileikovsky, 1962). To explain this absence of larvae, Mileikovsky proposed that the adults reproduce at greater depths, implying that the adults and larvae should be found together at depths below 500 m. To test this hypothesis, two series of vertical tows were taken during August of one year in the Kurile-Kamchatka trench (Mileikovsky, 1969). Here adults were most numerous from 200 m to 1000 m and larvae from 300 m to 2000 m (Mileikovsky, 1969). These data were then interpreted as substantiating the above hypothesis that adults and larvae are found in the same depth range below 500 m (Mileikovsky, 1969). However, in light of the information now available from the Arctic ocean, the sampling program in the Kurile-Kamchatka trench may not have been sufficient to unequivocally delimit the vertical distribution of the larvae and adults. For instance, only two sets of tows in one month of one year were taken. Secondly, the lengths of the tows in the first set of samples covered too great a vertical distance. Thirdly, the number of animals listed for each depth interval in both series is uncorrected for differences in the lengths of the tows. Fourthly, it is not clear that the same number of tows was taken at each depth. Thus, the data from the Kurile-Kamchatka trench may not be inconsistent with the pattern present in the Arctic ocean, in which the larvae are found deeper than the adults.

On the other hand, it is possible that the vertical distribution of the larvae and juveniles relative to the adults may in part vary with the oceanic region in question in accordance with factors not yet appreciated, for there are some observations in the literature which are difficult to reconcile with the view put forth in this paper. For instance, young approximately 2 mm long were found in the same sample with mature adults in a 11 m tow taken near Hut Point, Antarctica (Ehlers, 1912). Friedrich (1950) also notes that samples with many individuals collected on deep tows in the Atlantic were either of just young animals or a mixture of young and mature, whereas no samples contained only adults. From these data Friedrich concluded that a small number of adults produce many offspring and that due to the negligible amount of turbulence they tend to remain together in the deep sea, and only slowly and passively disperse. Thus, although Friedrich confirms the presence of young in deep water, he apparently would disagree with the idea that the adults spawn in shallower water than that subsequently occupied by the larvae. In this case, however, any apparent contradiction cannot be resolved, because we do not know the exact size of the immature specimens and too few such samples were found by Friedrich to be certain that he presents a general case. On the other hand and in apparent support of deep living ovigerous individuals, three females with ova were collected between 750 m and 1250 m in the north Atlantic at two separate stations (Støp-Bowitz, 1948). However, only 5 specimens of this species in total were collected on the entire cruise and none of these were reported as immature. Another somewhat ambiguous picture of the vertical distribution of the adults versus the juveniles emerges from the work of Hardy and Gunther (1935) from South Georgia, Antarctica. From November to May the vertical distribution of the adults of *P. longicirrata* from 50 m to 1000 m tended to overlap the vertical distribution of the juveniles of all species of polychaetes collected. Although most of the juveniles were thought by the authors to be *P. longicirrata,* the fact that all species were lumped together in their data and that we again do not know the relative sizes of the juveniles precludes a critical evaluation of their results.

Finally, Tebble (1960) has found independent support for the contention made here that *P. longicirrata* is capable of seasonal changes in its vertical position.

Examining data collected by a vertical closing net on a transect following the Greenwich meridian from 70° S to 35° S, he determined that during the summer and early fall from November to April *P. longicirrata* was most abundant in the upper 100 m, but that during the winter it migrated into deeper water where it was fairly abundant throughout the year. Tebble speculates that its presence in the surface waters may be for purposes of breeding and feeding, although he presents no data to support these possibilities.

It is, of course, tempting to directly compare and discuss the vertical distribution of the adults of *P. longicirrata* with that found by others such as Tebble (1960), Gunther and Hardy (1935), and Mileikovsky (1962 and 1969) in different parts of the world. That temptation, however, is resisted for many of the reasons stated earlier in this paper. More productive comparisons can hopefully be made when the results on other groups of planktonic organisms collected in the same program from Fletcher's Ice Island T-3 become available.

In conclusion, the occurrence of the larvae below the adults is an interesting and even a bit unusual, because as Marshall (1954) notes, the larvae of most species are either found above or in the same range as the adults. With *P. longicirrata* one can presently only speculate on an explanation for this phenomenon. One possibility, however, is that living deeper may reduce predator pressure when the larvae are too young to feed and thus unable to exploit the surface waters.

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Summary

During a two year period the vertical distribution of *Pelogobia longicirrata* (Polychaeta, Annelida) in the central Arctic ocean changed seasonally in conjunction with the relative age of the organisms. Adults with thirteen or more segments were primarily found throughout the year from 100–500 m. The peak occurrence of oocytes in the two month period of May/June was followed by a rapid decline in July/August, suggesting a spawning season in early summer or late spring. Larvae subsequently appeared below 500 m where specimens with one to three segments accounted for most of the animals collected between 900 m and 1200 m. Specimens with six or more segments were the youngest observed to have a mouth, anus, a continuous digestive tract, and a muscled pharynx, indicating that larvae smaller than these are probably incapable of feeding. They may instead live off of stored yolk retained from the egg. It is suggested that as the larvae mature they move up the water column and eventually join the adult population. The number of animals collected throughout the two years varied somewhat without demonstrating any apparent seasonal trends. The mean density from 0–1500 m was 46/1000 m^3 in 1970 and 37/1000 m^3 in 1971.

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